THE FOSSIL FLORA OF MELVILLE ISLAND, NORTHERN AUSTRALIA

MIKE POLE

Department of Plant Science, University of Tasmania
G.P.O. Box 252C, Hobart , TAS 7001, Australia

ABSTRACT

Twenty-seven angiosperm taxa and two conifers are described from the Van Diemen Sandstone of Melville Island, Northern Territory. The angiosperms include *Brachychiton*, *Grevillea*, *Melaleuca*, and probable Cunoniaceae. The conifers are *Araucaria* and an unidentified genus of the Cupressaceae. Floristics and physiognomy suggest the climate was neither megathermal nor microthermal but that rainfall may have been seasonal. Two distinct assemblages are present, one from clay-rich mud, the other from sandier lithologies. The age of the Van Diemen Sandstone, which was probably deposited by a perennial sinuous river, is not known more precisely than Tertiary, but is suggested here to be Paleogene.

KEYWORDS: Plant macrofossils, Tertiary, *Araucaria*, Proteaceae, Paleogene

INTRODUCTION

Almost all the knowledge of Australia's vegetation history during the Tertiary, when angiosperms had reached the world-wide prominence they have today, comes from the south-eastern corner of the country. A few localities are known along the southern edge of the mainland, in Western Australia, and in southern and central eastern Queensland. There are even a few bore hole samples with fossil pollen from central Australia. But the vast area that remains - essentially the northern half of Australia - is a virtual blank in time for over 80 million years. This is frustrating, for although the record elsewhere is excellent, it is half a continent away and almost certainly would have lain in a completely different climatic belt. Palaeontologists are naturally curious to know what was happening in the presently tropical latitudes as well as the temperate ones. This gap in the record places great importance on the one locality that is known – Cape Van Diemen at the north-west tip of Melville Island, which lies north of Darwin (Fig. 1). Fossils from this location were first described by White (1974), and from the results of a brief collection made by D. Bowman (Pole and Bowman 1996). The fossils are poorly preserved, lacking organic preservation and with little chance of

including pollen, but this was to be expected in a region enduring a hot, monsoonal weathering regime. While not expecting any miracles of preservation, intensive collection would likely add more taxa, more complete specimens, perhaps more localities, and maybe indicate something in the geology that would help to date the deposit. This stimulated support for a major expedition which formed the basis of this paper.

GEOLOGY

The Van Diemen Sandstone forms approximately 17.5 m high coastal cliffs of the eastern side of Cape Van Diemen. The sediments are essentially flat-lying, though there may be some gentle warping. The top two or three metres are dark red and form the uppermost part of a lateritic weathering profile. Slope-wash of this red material frequently obscures parts of the cliff and makes continuity of bedding difficult to observe.

A schematic indication of the geology is shown as Figure 2. The lower ten metres or more are predominantly formed of tabular cross-bedded sands. The apparent direction of flow of most beds in the cliff face is from south east to north west. Exposures at right angles to the cliff line show most movement
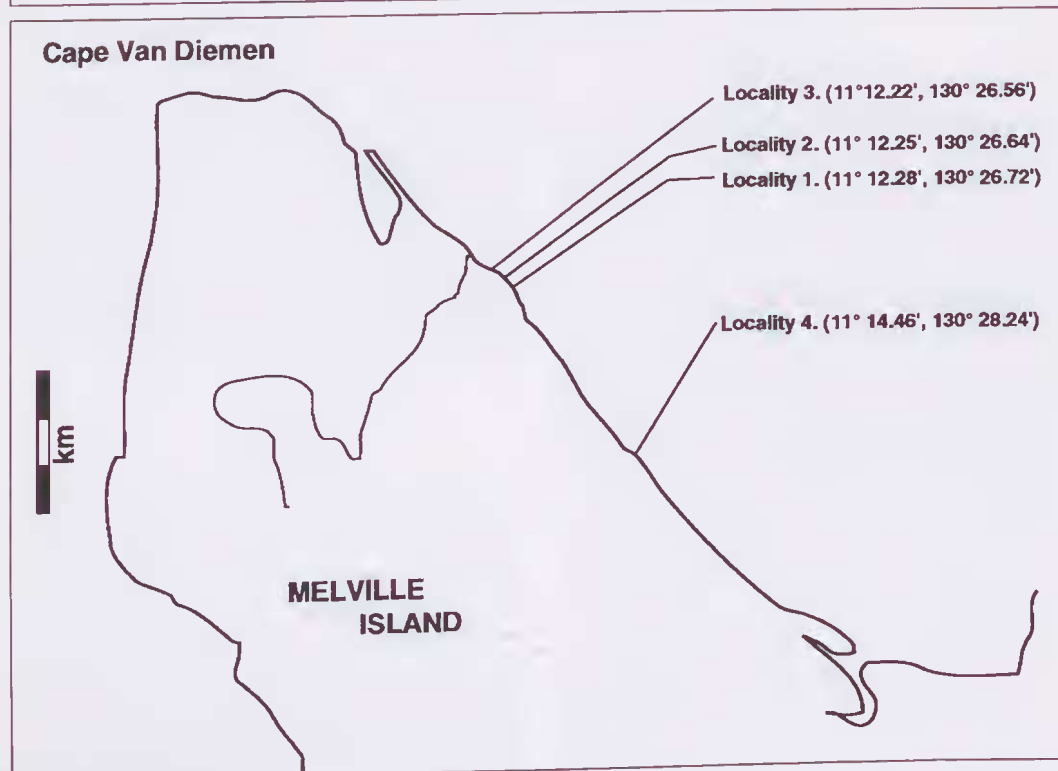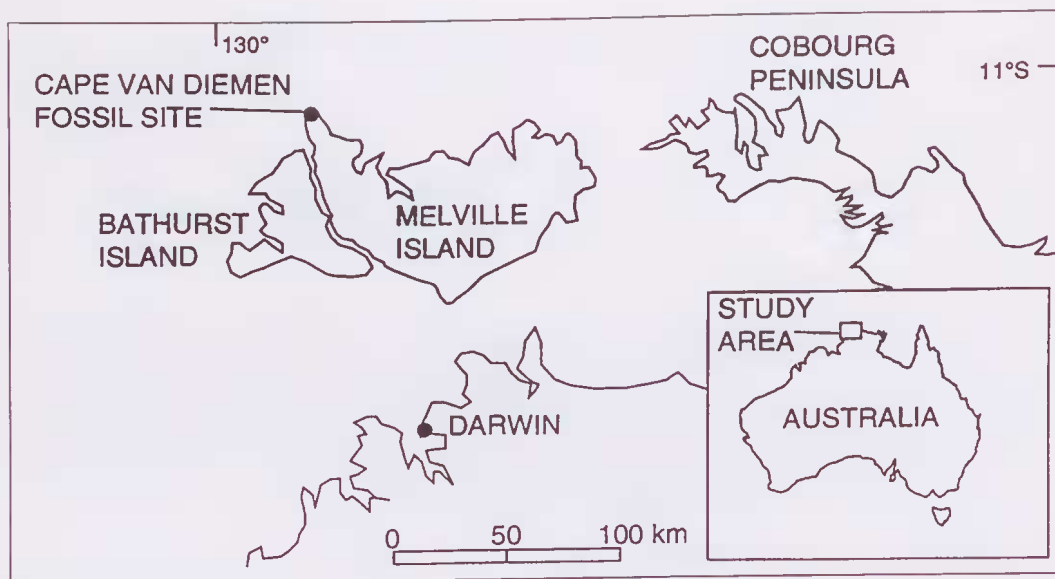
Fig. 1. Locality map.

was away from the coast, i.e., a south-westerly direction. This indicates the dominant true direction of flow was generally westerly. One bed had overturned forsets.

Higher in the cliff, discrete lensoid bodies of sediment contain the bulk of the plant fossils. The lenses appear to be shallow channels which were cut into the underlying sandstone, though in detail, a clear erosional base is not always clearly seen. It was not practical to collect fossils directly from these lenses (extraction was too hard) but boulders forming the talus below were readily
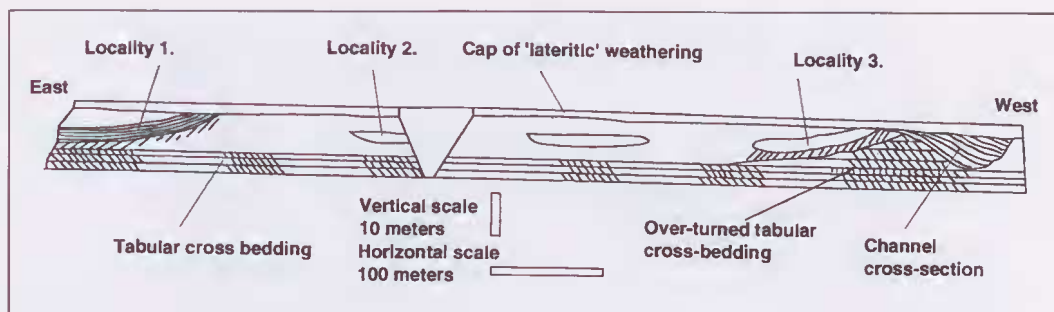
Fig. 2. Schematic geology.

accessible and clearly derived from the lenses. Collecting concentrated on four lenses, designated localities 1-4. Lenses 1-3 were numbered in a westerly direction, Locality 4, much further to the east, was discovered later. The assemblage described in Pole and Bowman (1996) comes from Locality 3. Within Locality 1, several boulders had a distinct lithology of soft, fissile, purple-coloured mud. Fossils are abundant in the 'purple mud' facies and fossils from this facies are treated as a separate assemblage. Other sediment coming from Locality 1, and from the other localities was heterogeneous, but generally much sandier.

To the west of Locality 3 a clear cross-section of a fluvial channel can be seen, which has been filled by lateral accretion. Another may exist between Locality 2 and 3. Fine-grained intraclast pebbles are common as lag accumulations at the base of the channels and at the base of many of the forsets.

These appear to be fluvial sediments deposited by a large, highly sinuous river with relatively continuous flow. This interpretation is based on:

a) the existence of the channel or channels, which are at right angles to the tabular cross-bedding at the base, indicating the change in flow direction as a fluvial meander cut its way into older channel sediments;

b) the lensoid bodies containing the plant fossils, which suggest cut-off meanders, or 'ox-bow' lakes;

c) the large amount of 'claystone' lag associated with channel bases and the bases of forsets. This suggests a large amount of overbank material and

constant reworking of the floodplain by migrating channels;

d) there is no evidence of ephemeral flow, which would be more typical of less sinuous, or braided fluvial systems, although the over-turned forsets do indicate that flow may have increased suddenly at times.

METHODS

This paper is the result of three days collecting on Melville Island by ten people in September 1994. The island was accessed by boat. Collecting was carried out using rock hammers, picks, and a pneumatic drill. Specimens were further exposed, where necessary, by a compressed-air powered chisel in the Department of Botany, University of Tasmania. Leaves were illustrated by tracing with a Nikon Profile Projector and then redrafting on architectural film, and by photography. The sediments are too deeply weathered to preserve cuticle or palynomorphs. All material collected on this expedition was catalogued and stored in the Museum and Art Gallery of the Northern Territory (numbers prefixed with 'P'). Specimens prefixed with SB were referred to in Pole and Bowman (1996), and are stored in the same place under P98123.

After grouping all specimens into taxa, and description, identification was attempted based on leaf architectural characters (following the terminolgy of Hickey 1973; Dilcher 1974; and with some modifications by Pole 1991) and using herbarium material and published illustrations. The formal taxonomy, including taxa described by Pole and Bowman (1996) is presented after the

following discussion on identification. To shorten descriptions, only instances where 'development' (sensu Pole 1991) deviates from 'normal', or where it is unclear, are mentioned.

Key indicating basis for angiosperm taxa

1. Leaves compound or specimen obviously a leaflet 2
1. Leaves simple or not obviously leaflets.......................................7

2. Unattached leaflet ovate, with curved, asymmetrical base ... Compound leaf G
2. Leaflets attached to form compound leaf 3

3. Leaf trifoliate .... Compond leaf E
3. Leaf pinnately compound 4

4. Leaflets petiolate ..... Compound leaf B
4. Leaflets sessile 5

5. Leaflets longer than 100 mm .... Compound leaf A
5. Leaflets shorter than 100 mm 6

6. Leaflets with small teeth .... Compound leaf D
6. Leaflets with large teeth .... Compound leaf C
6. Leaflets with deep sinuses .... Compound leaf F

7. Leaves lobed 8
7. Leaves entire 9
7. Leaves toothed 12

8. Leaves deeply dissected, pinnatisect .... *Grevillea*
8. Leaves deeply bilobed .... cf. *Dilobeia/Liriodendrites*
8. Leaves with five radiating lobes .... *Brachychiton*

9. Major venation of about three orders of (apparently) longitudinal veins 10
9. Major venation not strong enough to be seen clearly...................................... 11
9. Major venation pinnate, 3-4 laterals each side, wide elliptic .... Entire Type C

10. Shape lanceolate .... *Melaleuca*
10. Shape ovate .... *Smilax*

11. L:W > 8, width < 10 mm .. Entire type A
11. L:W > 8, width > 10 mm ... Entire type F
11. Shape elliptical (L:W about 2) .... Entire type B
11. Shape oblong .... Entire type D
11. Shape obovate, with tapering base .... Entire type E

12. Teeth recumbent with prominent glandular apex .... Toothed Margin Type A12
12. Teeth without prominent glandular apex 13

13. Shape lanceolate or very narrow elliptic (L:W >8) 14
13. Shape narrow ovate or wide elliptic (L:W<3) 16

14. Teeth prominent, about 1.5 m high .... Toothed Margin Type J
14. Teeth low, 1 mm high or less 15

15. Lateral venation high angle, very closely spaced .... Toothed Margin Type F
15. Lateral venation low angle, loose, disorganised ......Toothed Margin Type C

16. Major venation externodromous .... Toothed Margin Type D
16. Major venation craspedodromous ... 17
16. Major venation unclear, apex bluntly triangular .... Toothed Margin Type G

18. Teeth large, triangular .... Toothed Margin Type B
18. Teeth small, erect .... Toothed Margin Type E

SYSTEMATICS

A complete list of all Melville Island specimens follows. This includes those described in Pole and Bowman (1996). These are not redescribed unless significant new material was found.

Possible fern

Branching shoots with leaves flattened into one plane on either side of an axis were dominant at Locality 4 (Fig. 3). The leaves are imbricate and have an open dichotomous venation. This suggests a fern, or fern-like plant. The superficial resemblance to
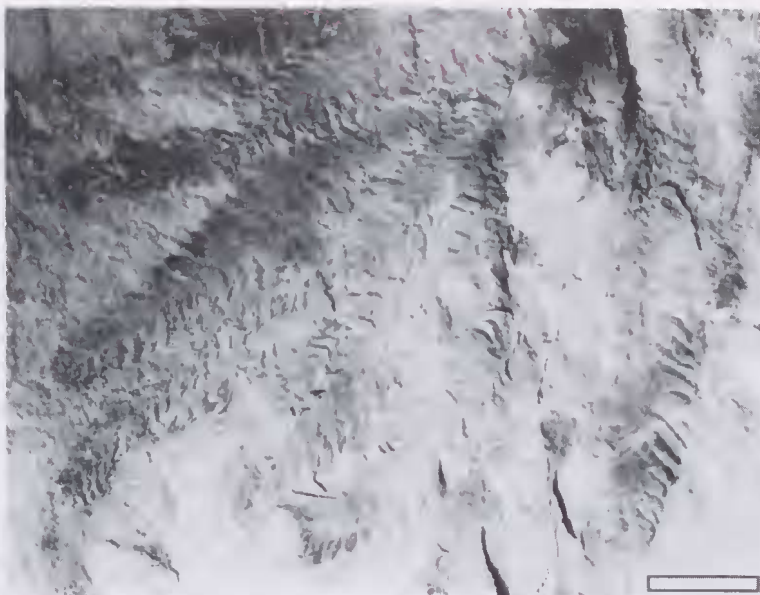
Fig. 3. ?Fern. P94327 (scale = 10 mm).

lycopods and conifers is ruled out by the venation, however placement within some extinct gymnosperms like Bennettitaleans is not ruled out.

?Fern
(Fig. 3)

Reference specimen. Locality 4: P94327.

Araucariaceae

Several shoots and a single detached leaf clearly belong to *Araucaria* (Fig. 4). At least two ovuliferous cone/seed complexes were recovered which presumably belong with the foliage, one of these has thin lateral wings indicating *Araucaria* section Eutacta. Three specimens which appear to be elongate structures of small, helically-disposed scales, may be male cones of *Araucaria*.

Araucaria sp.
(Fig. 4)

Referred material. Locality 1: shoots P94217, P94219, P94220, P94224; leaf P94223; ovuliferous cone scale: P94216, P94218; ? male cones P94221, P94222. Locality 3: detached leaf P94303; ovuliferous cone scale P94300, P94311.

Description. Shoots with triangular, slightly flattened, scale-like leaves. Ovuliferous cone scale with thin lateral wings.

Cupressaceae

An additional specimen of a shoot with opposite-decussate leaves described as Cupressaceae by Pole and Bowman (1996) was recovered.

Cupressaceae gen. et sp. indet.
(Pole and Bowman 1996)

Referred material. Locality 1: P94117, P94191-P94193. Locality 2: P94262. Locality 3: SB916, SB917, SB973.

Proteaceae

Several deeply dissected leaves regarded by White (1974, 1976) and Pole and Bowman (1996) as *Grevillea* were recovered (Fig. 5). The new material suggests more than one species may be represented, but there are not enough specimens to confirm this.

Many more specimens of *cf. Dilobeia* (Pole and Bowman 1996) were recovered including one nearly perfect example (Fig.
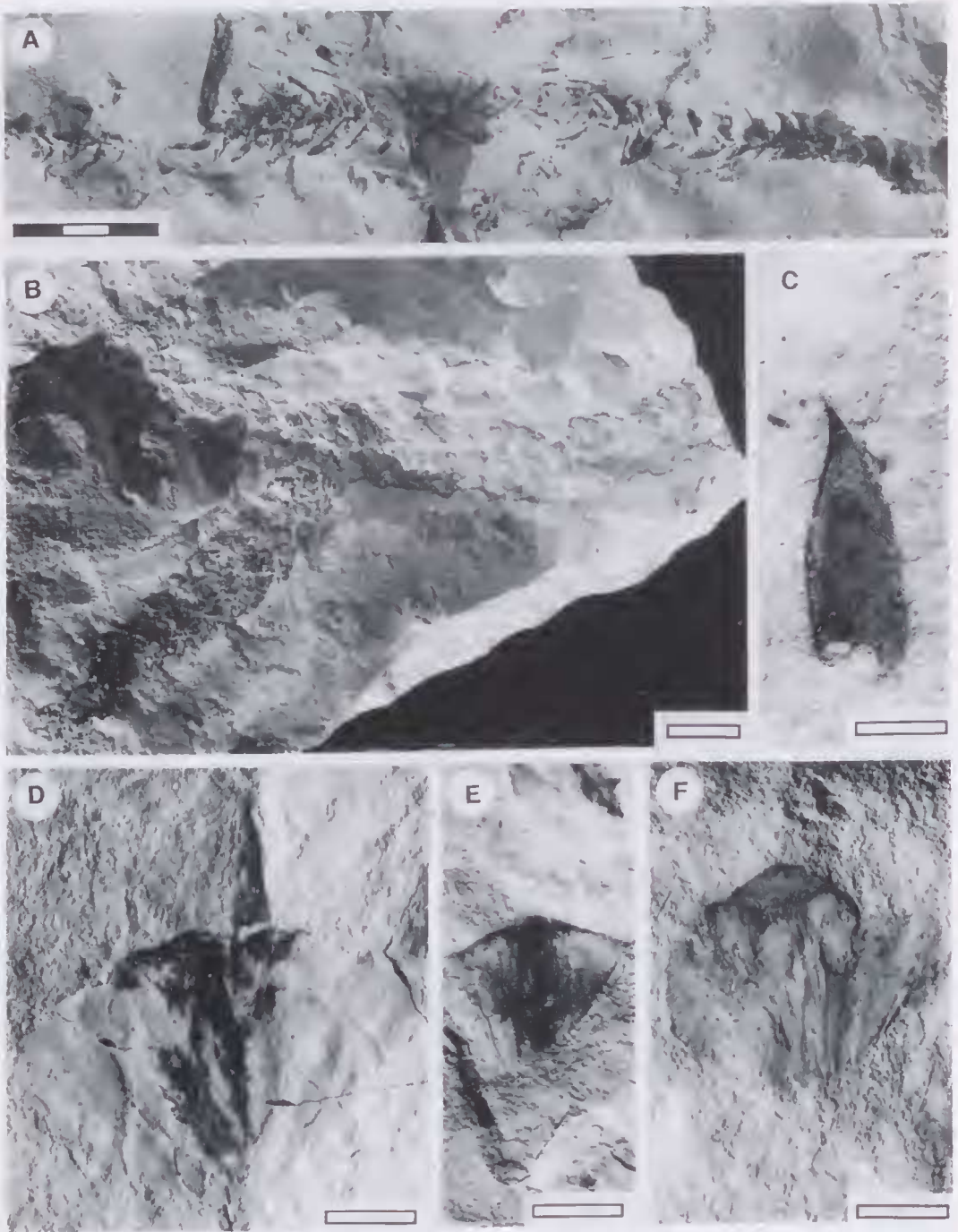
Fig. 4. *Araucaria* sp. **A**, shoot, P94224 (scale = 30 mm); **B**, shoot, P94219; **C**, leaf, P94303; **D**, ovuliferous scale, P94311; **E**, ovuliferous scale, P94218; **F**, ovuliferous scale, P94216 (B-F, scale = 10 mm).
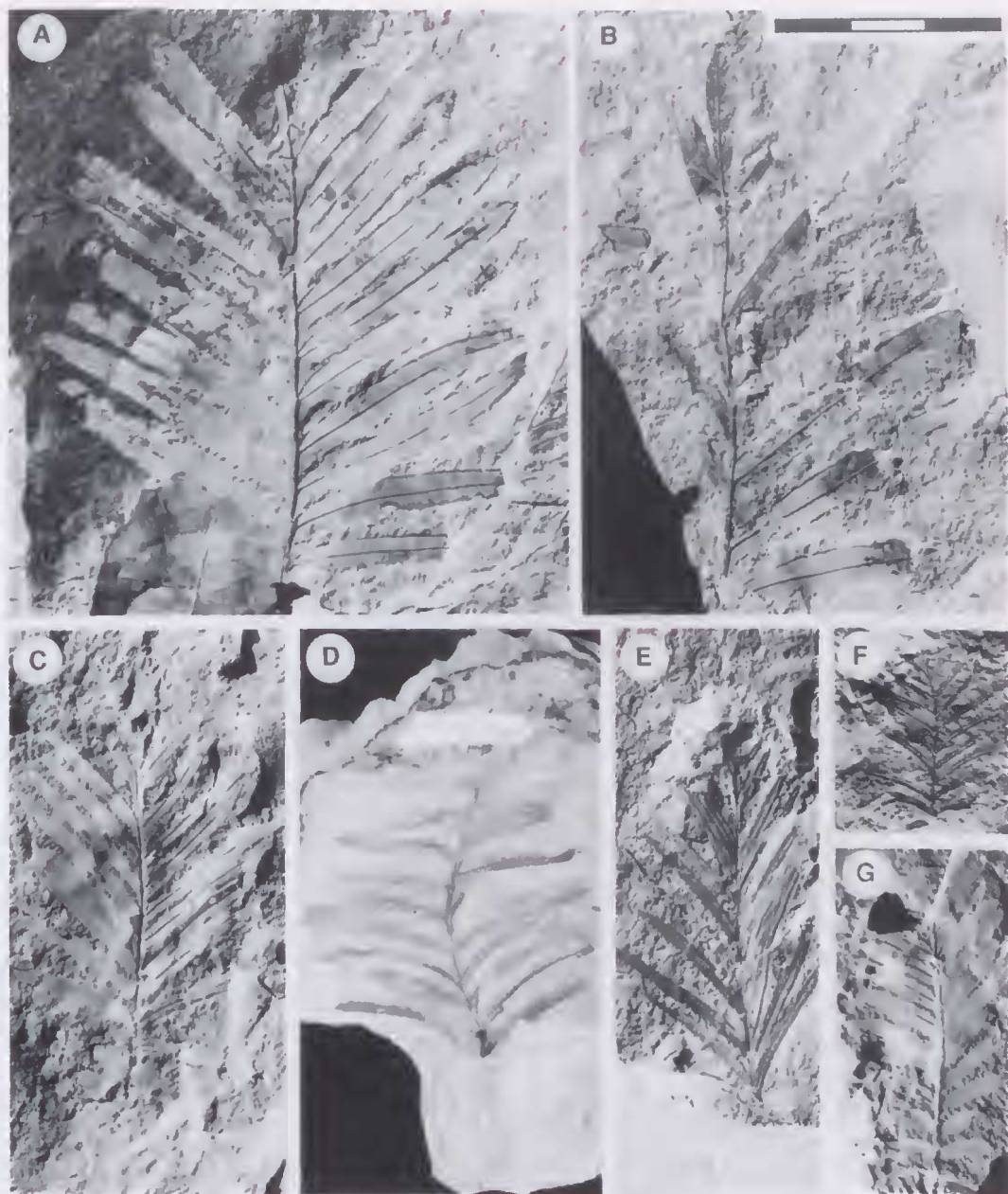
Fig. 5. *Grevillea* sp. cf. *G. whitiana*. **A**, P94122; **B**, P94125; **C**, P94169; **D**, P94167; **E**, P94271; **F**, P94270; **G**, P94101 (scale = 30 mm).

6). The extinct genus *Liriophyllum* Lesq. emend. Dilcher and Crane (1984) from the mid Cretaceous of the USA is rather similar in having a bilobed lamina but was not discussed by Pole and Bowman (1996). It differs from the Melville Island fossils in having a stout midrib extending to the base of the sinus and forking into two prominent veins, distinct from the secondary veins below, which form the leaf margin typically for about 0.3–0.16 of the lobe length. Above this point the lamina arches away from the vein into the sinus and broadens distally to form each lobe (Dilcher and Crane 1984). In
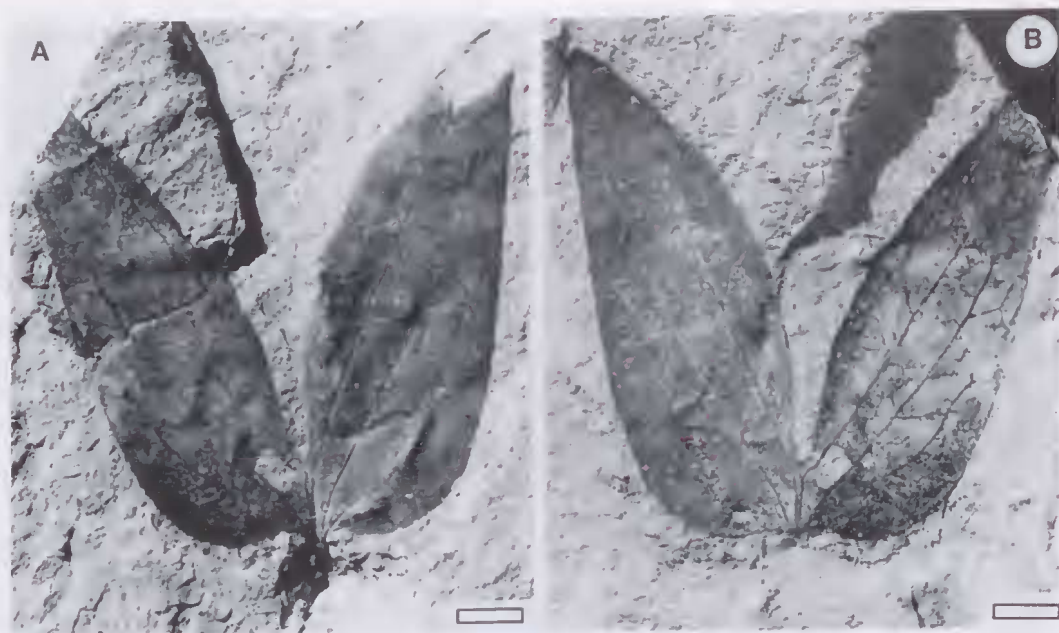
Fig. 6. *cf. Dilobeia/Liriodendrites*, P94297, **A**, part; **B**, counterpart (scale = 10 mm).

the new fossils, the midrib is quite reduced when it reaches the sinus, there is no sign of it forking, and there is no pronounced arching of the lamina into the sinus (forming counter-external veins sensu Pole 1991). In a recent paper, Johnson (1996) described a new bilobed leaf genus, *Liriodendrites*, from the latest Cretaceous of the USA. The description of this genus clearly covers the Melville Island fossils. However, while *Liriodendrites* was assigned to the Magnoliales, and perhaps to the Magnoliaceae, the generic description would also include the extant Proteaceae genus *Dilobeia*, to which the Melville Island fossils have been compared. This raises a taxonomic problem—whether to continue to refer to the new fossils informally as *cf. Dilobeia*, or to place them in the genus *Liriodendrites*, which, if the American fossils are correctly placed in the Magnoliales, is not a natural group. My taxonomic philosophy is not to formally use genera which are not natural. The Melville Island leaves will continue to be referred to informally as *cf. Dilobeia/Liriodendrites*.

Grevillea sp. *cf. G. whitiana*
(Pole and Bowman 1996).
(Fig. 5)

Referred material. Locality 1: P94101, P94104–P94106, P94167–P94175. Locality 2: P94261, P94270, P94271, P94274. Locality 3: P94122, P94123, P94125, P94314–P94317, P94324, P94325, SB945, SB962, SB966, SB967.

Grevillea sp. *cf. G. longifolia*
(Pole and Bowman 1996)
Referred specimen. Locality 3: SB943.

Grevillea sp. *cf. G. dryophylla*
(Pole and Bowman 1996)
Referred specimen. Locality 3: SB955.

cf. *Dilobeia* / *Liriodendrites*
(Fig. 6)

cf. Dilobeia (Pole and Bowman 1996)
Referred material. Locality 1: P94102, P94112, P94114, P94145. Locality 2: P94259. Locality 3: P94286–P94297, SB951, SB952, SB1048.

Smilacaceae

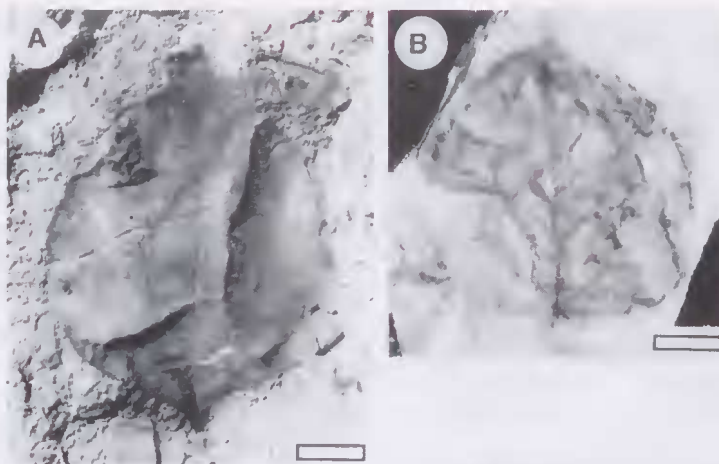Leaves are common in the 'purple mud' facies of Locality 1 which show the typical

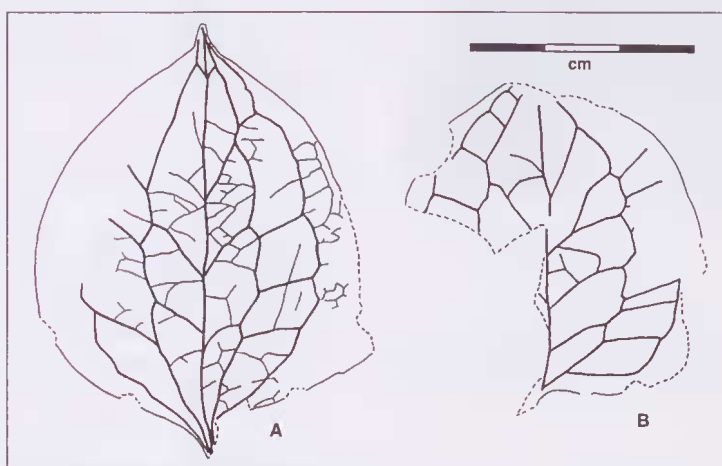Fig. 7. *Smilax* sp. **A**, P94143; **B**, P94135 (scale = 10 mm).

Fig. 8. *Smilax* sp. **A**, P94135; **B**, P94143.

venation of the Smilacaceae (Figs 7–8). This consists of a pair of veins which arch directly from the petiole to the apex (these may not be longitudinal veins in the true sense as they may branch downwards, and veins which connect them with the midrib may be of the same order) and these two veins are flanked by a wide looping zone with three well-developed orders of loops. They are identified as *Smilax* by direct comparison with some extant species. There are seven species of *Smilax* in Australia (Conran and Clifford 1986) and more in the areas to the north in the Malaysia-New Guinea region, so it would be premature to identify the fossils or describe a new species on the poorly preserved material available.

Smilax sp.
(Figs 7–8)

Reference specimen. Locality 1: P94143.

Referred material. Locality 1: P94129–142, P94151, P94158–P94162, P94182, P94202, P94203, P94205, P94206, P94207, P94210–P94212, P94215.

Description. Leaf size: length 22–65 mm, width 13–58 mm. Leaf shape: simple, wide ovate to very wide ovate (a juvenile
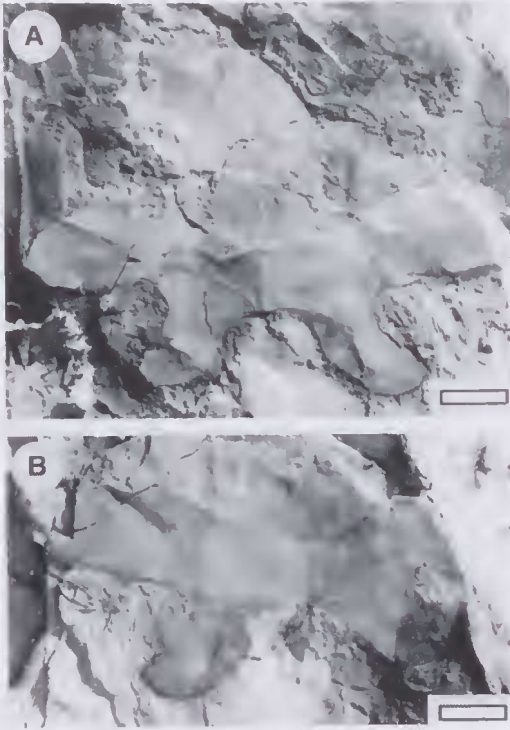
Fig. 9. *Brachychiton* sp. A, P94150, part; B, P94150, counterpart, showing petiole (scale = 10 mm).

specimen is wide obovate); apex rounded but finishing acutely; base rounded but finishing acutely. Margin entire.

Sterculiaceae

Two leaves compare well with some extant species of *Brachychiton* (Figs 9–10). They are palmate with five, entire margined lobes, with basal laterals paired at the base. The petiole is preserved at an angle to the midrib which is taken to indicate presence of an apical pulvinus. In an Australian context, there is little to confuse this form with, although some foreign *Passiflora* are similar. Guymer (1988) monographed *Brachychiton* and the fossils may be compared with his figures. The most similar species, with regard to five lobes which expand slightly in the middle, and a cordate base, is *B. bidwillii* Hook. The Melville Island fossil appears distinct in having a broad sulcus at the base, rather than a sharp notch.

Brachychiton sp.
(Figs 9–10)

Reference specimen. Locality 1: P94150.
Referred material. Locality 1: P94144.
Description. Leaf size: length 25–48 mm, lobe width 9–19 mm. Leaf shape: simple, palmatisect (five lobes), apex obtuse, base cordate, sinuses smooth, petiole lying at an angle to midrib, length unknown. Margin entire.

Myrtaceae
Melaleuca sp.
(Pole and Bowman 1996)

Referred material. Locality 1: P94111, P94148, ?P94152, P94154, P94156, ?P94157, P94178, P94180, P94189, P94184, P94204, ?P94208, P94209, P94214. Locality 3: P94307, SB944, SB946–SB949.

? Leguminosae

A possible flattened branch or cladode system, was found (Fig. 11). This is similar to some Leguminosae, but no detailed comparison has been made.

Flattened branch/cladode
(Fig. 11)

Reference specimen. Locality 2: P94187.
Description. A central axis, preserved length 65 mm, 2–3 mm wide, with at least three lateral branches. Two of the lateral branches branch again. The structure shows a broad similarity to flattened branches, or cladodes, for instance those found in the Leguminosae. The branches narrow slightly towards the main axis, there is surface detail of longitudinal striations separated by nodes.

Family indet.
Simple Entire Margined Leaves
(Figs 12–13)

These have been subdivided quite subjectively, but Entire Margin Type A forms a clear group. These, and perhaps Entire
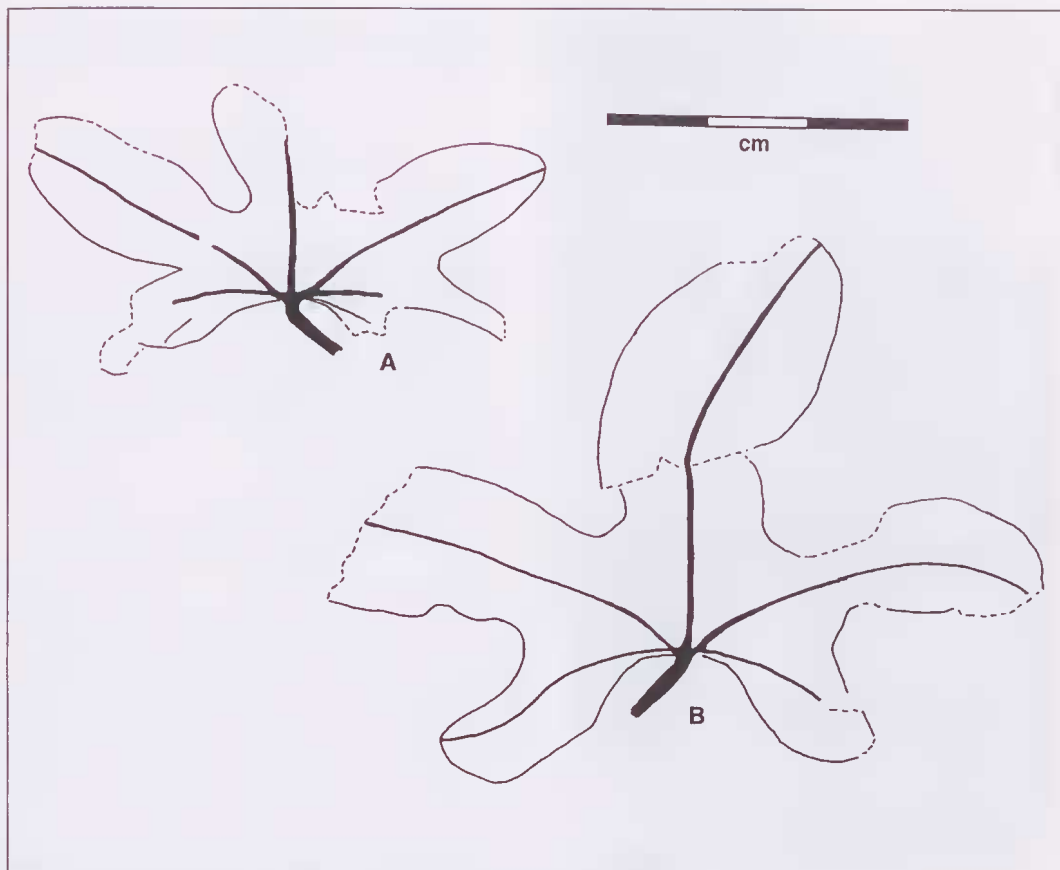
Fig. 10. *Brachychiton* sp. A, P94144; B, P94150.

Margin Type F are putative *Eucalyptus*, but other possibilities exist, such as Proteaceae, or even *Podocarpus* in the case of Type A.

Entire Margin Type A
(Fig. 12)

Reference specimen. Locality 3: P94302.
Referred material. Locality 1: P94153, P94163, P94181, P94183, P94188, P94194, P94198, P94200, P94201. Locality 2: P94265, P94266. Locality 3: P94301, P94302, P94304–P94309, P94312, P94323.
Description. Leaf size: length 50–120 mm, width 3-5 mm. Leaf shape: simple, lanceolate or very narrow elliptic (L:W >8), apex attenuate, base decurrent, petiole 2–3 mm long. Margin entire. Development unclear.

Entire Margin Type B
(Fig. 13A, C)

Reference specimen. Locality 2: P94257.
Referred material. Locality 1: P94238. Locality 2: P94176.
Description. Leaf. size: length about 80 mm, 25 mm. Leaf shape: simple, elliptical (L:W about 2), apex acute, base unknown, petiole unknown. Margin entire. Venation externodromous.

Entire Margin Type C
(Fig. 13B)

Reference specimen. Locality 1: P94113.
Description. Leaf size: length 21 mm, width 12 mm. Leaf shape: wide elliptic, apex probably obtuse, base obtuse, petiole absent.

Fig. 11. ?Legume/cladode. P94187 (scale = 10 mm).

Margin entire. Venation: externodromous. Three or four laterals on either side of midrib.

Entire Margin Type D
(Fig. 13D)

Reference specimen. Locality 1: P94195. **Description.** Leaf size: length 66 mm, width 18 mm. Leaf shape: oblong, apex obtuse, base obtuse, petiole unknown. Margin entire.

Entire Margin Type E
(Fig. 13E)

Reference specimen. Locality 1: P94196. **Description.** Leaf size: length 45 mm,

width 14 mm. Leaf shape: wide elliptic, apex obtuse, base tapered, petiole normal. Margin entire. Development unclear.

Entire Margin Type F
(Fig. 13F–J)

Reference specimen. Locality 1: P94194. **Referred material.** Locality 1: P94163, P94188, P94194, P94201, P94331.

Description. Leaf size: length 60–>100 mm, width 10–17 mm. Leaf shape: lanceolate, apex probably attenuated, base acute, petiole normal. Margin entire. Development unclear.

Simple Toothed Margin Leaves
(Figs 14–16)

Along with *Smilax*, 'Toothed Margin Type A' is the most common leaf type in the purple mud facies of Locality 1. It has a distinct cuneate base, with a moderate length petiole (Figs 14–15). The marginal teeth have distinct glandular tips. Lateral venation is closely spaced, without the typical, well-spaced laterals of most pinnate leaves. *Ceratopetalum* (Cunoniaceae) is a likely identification of the Toothed Margin Type A taxon. A pulvinus is present at the base of the lamina in some species, such as *C. apetalum*, but is absent on the fossil. It is similar in outline to the taxon which White (1974, 1976) identified as *Ceratopetalum* sp., but as well as the teeth being glandular (not observed on the White specimen), the teeth and sinuses in between are more rounded.

Toothed Margin Type E (Fig. 16D) is suggested to be Cunoniaceae. It has craspedodromous venation, where the laterals bisect the margin at the apical edge of small, erect teeth. It may be a leaflet of *Cunonia* or *Weinmannia*, but other genera in the family are not ruled out.

Toothed Margin Type A
(Figs 14, 15)

Reference specimen. Locality 1: P94233. **Referred material.** Locality 1: 94107, P94108, P94116, P94119, P94120, P94121, P94149, P94155, P94164, P94179, P94186,
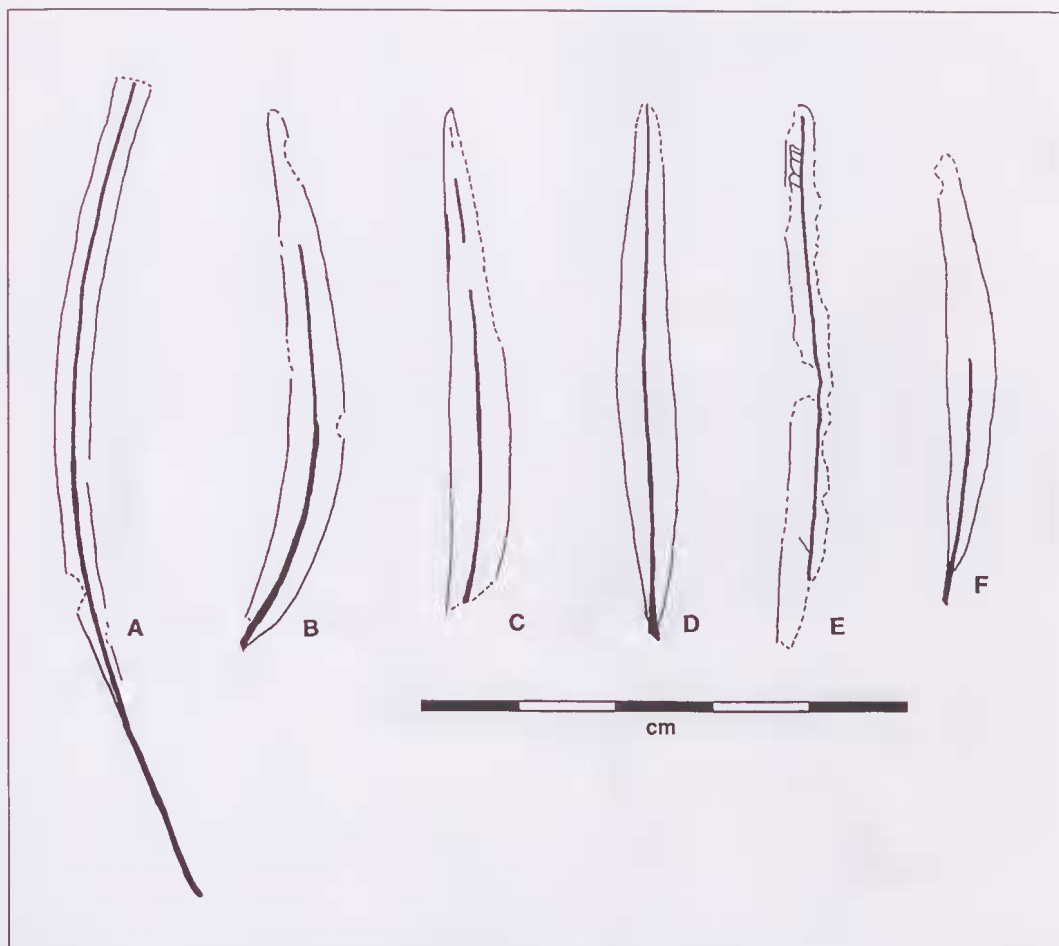
Fig. 12. A, Entire Margin A, P94265; **B**, Entire Margin A, P94302; **C**, Entire Margin A, P94304; **D**, Entire Margin A, P94301; **E**, Entire Margin A, P94305; **F**, Entire Margin A, P94312.

P94225–P94237, P94239–P94252. Locality 2: P94260, P94264, P94268. Locality 3: P94321

Description. Leaf size: length 45–160 mm, width 19–84 mm. Leaf shape: lanceolate, apex attenuate, base cuneate, petiole 15–20 mm. Margin non-entire (toothed), with prominent glands at tooth apices, tooth height about 1 mm, recumbent, spacing about 2–5 mm. Venation externodromous.

Toothed Margin Type B
(Fig. 16 A)

Reference specimen. Locality 1: P94103.

Referred material. Locality 2: P94254. Locality 3: P94318.

Description. Leaf size: length 18–33 mm, width 5–7 mm. Leaf shape: not clear, possibly a fragment of a simple, lorate or linear leaf, apex unknown, base unknown, petiole unknown. Margin non-entire (toothed), tooth height about 1 mm, inclined, spacing about 4 mm. Venation craspedodromous.

Toothed Margin Type C
(Fig. 16B)

Reference specimen. Locality 1: P94197.
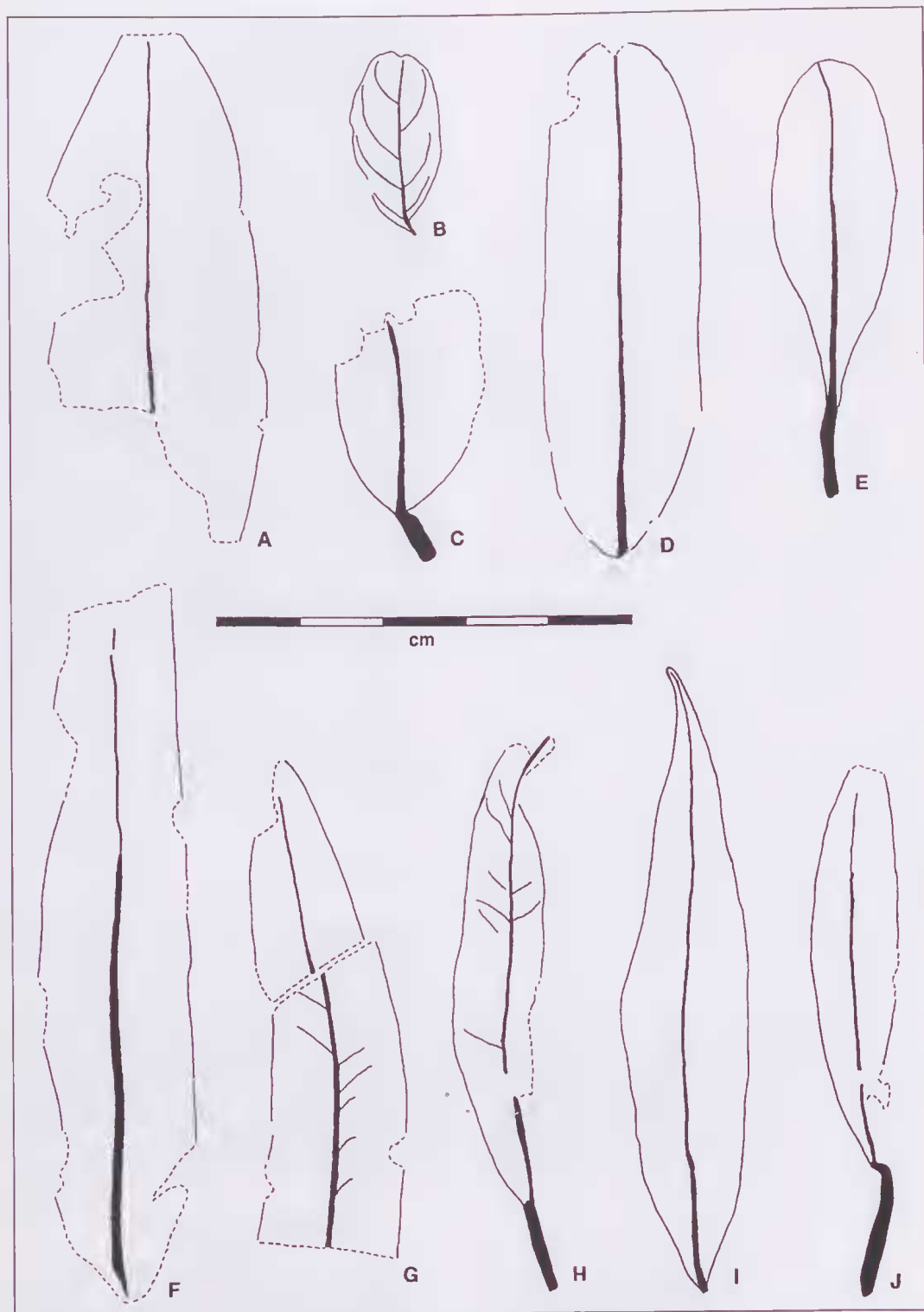**Description**. Leaf size: length 35 mm, 19 mm. Leaf shape: very narrow elliptic, or

Fig. 13. A, Entire Margin B, P94257; **B**, Entire Margin B? P94176; **C**, Entire Margin C, P94113; **D**, Entire Margin D, P94195; **E**, Entire Margin E, P94196; **F**, Entire Margin F, P94163; **G**, Entire Margin F, P94331; **H**, Entire Margin F, P94201; **I**, Entire Margin F, P94194; **J**, Entire Margin F, P94188.
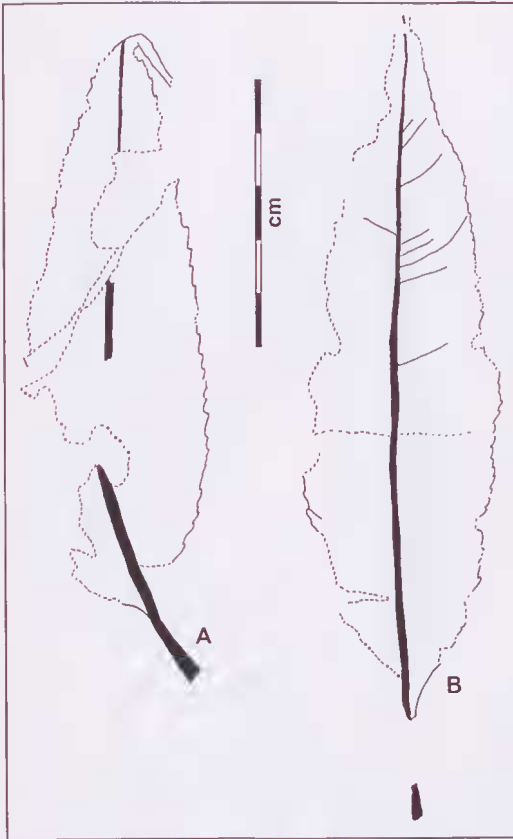
Fig. 14. Toothed Margin A. **A**, P94233; **B**, P94234.

narrow oblanceolate, apex unknown, base unknown, petiole 2–3 mm. Margin non-entire (toothed), tooth height 0.5 mm, spacing 2–3 mm. Venation not clear.

Toothed Margin Type D
(Fig. 16C)

Reference specimen. Locality 1: P94185.
Referred material. Locality 3: P94319
Description. Leaf size: length 26–35 mm, width 10–16 mm. Leaf shape: narrow ovate, apex acute, base obtuse, petiole absent. Margin non-entire (toothed), tooth height 0.2 mm, spacing 2–3 per mm. Venation externodromous.

Toothed Margin Type E
(Fig. 16D)

Reference specimen. Locality 1: P94147.

Referred material. Locality 1: P94115, P94118. Locality 3: P94313, P94322.
Description. Leaf size: length estimated 80 mm, width 32–40 mm. Leaf shape: wide elliptic, apex unknown, base obtuse, petiole absent. Margin non-entire (toothed), tooth height 0.2 mm, erect, spacing about 1–2 mm. Venation craspedodromous.

Toothed Margin Type F
(Fig. 16 E, F)

Reference specimen. Locality 3: P94299.
Description. Leaf size: length 105 mm, width 11 mm. Leaf shape: linear or lorate, apex probably attenuate, base unknown, probably decurrent, petiole unknown. Margin non-entire (toothed), tooth height about 1 mm, spacing about 4–5 mm. Venation not clear.
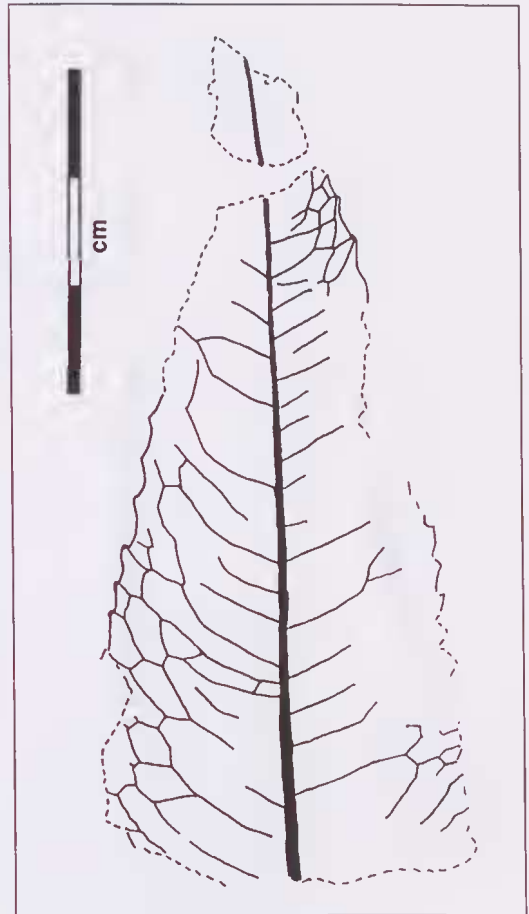

Fig. 15. Toothed Margin A. P94119.

Fig. 16. A, Toothed Margin B, P94103; B, Toothed Margin C, P94197; C, Toothed Margin D, P94185; D, Toothed Margin E, P94147; E, Toothed Margin F, P94299; F, Toothed Margin F, P94254; G, Toothed Margin G, P94128; H, Toothed Margin H, P94253; I, Toothed Margin I, P94213; J, Toothed Margin J, P94320.
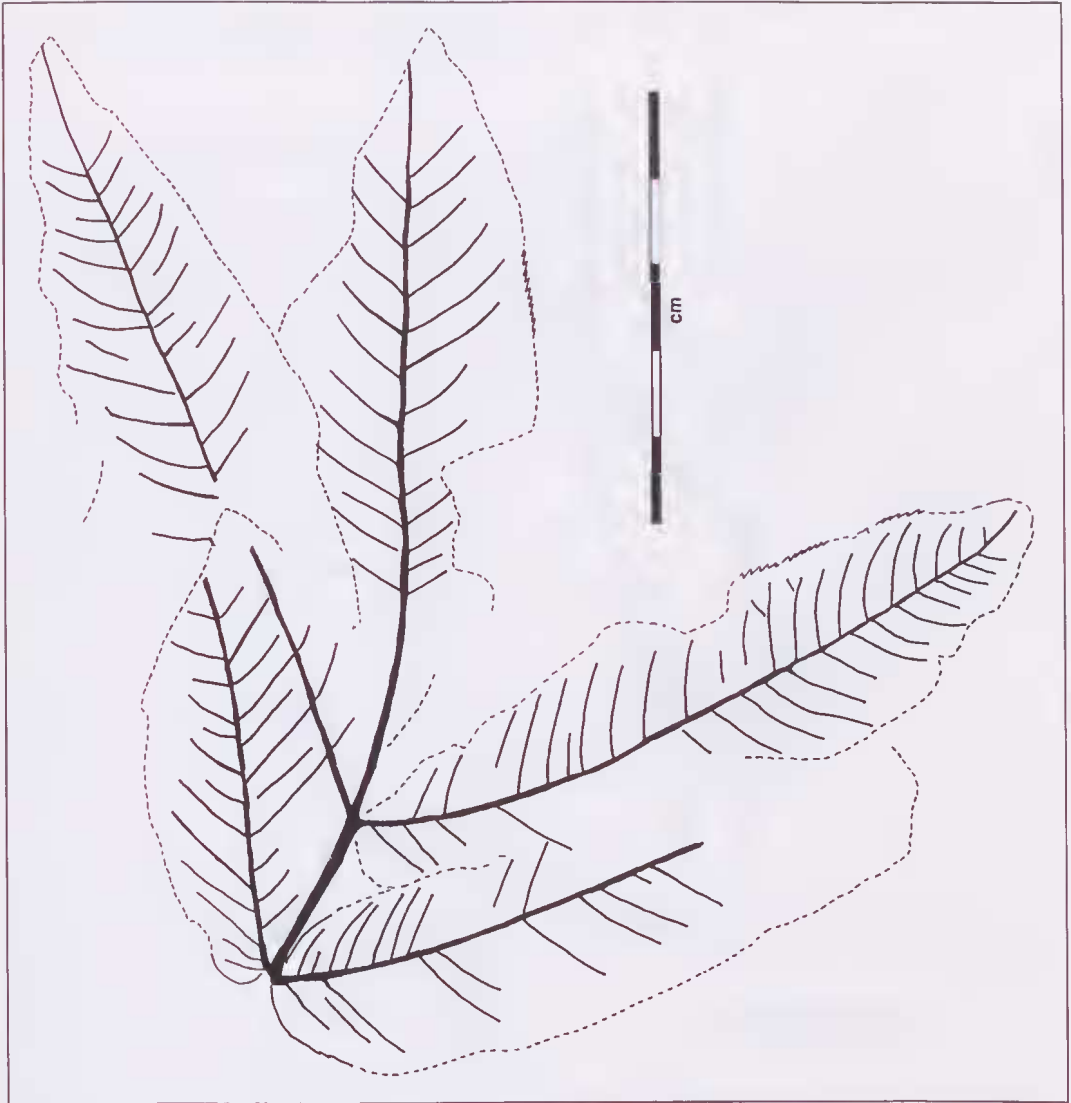
Fig. 17. Compound Leaf A, P94277.

Toothed Margin Type G
(Fig. 16G)

Reference specimen. Locality 1: P94128.
Description. Leaf size: length unknown, preserved length 30 mm, width about 24 mm. Leaf shape: unknown, apex possibly acute, base unknown, petiole unknown. Margin non-entire (toothed), tooth height 2–4 mm, spacing about 7 mm. Venation craspedodromous.

Toothed Margin Type H
(Fig. 16H)

Reference specimen. Locality 2: P94253.
Description. Leaf size: length 65 mm, width 13 mm. Leaf shape: lanceolate, apex attenuate, base obtuse, petiole 1 mm. Margin non-entire (toothed), tooth height about 0.1–0.2 mm, erect, spacing about 1 mm. Venation externodromous.

Fig. 18. Compound Leaf A, P94124.

Toothed Margin Type I
(Fig. 16I)

Reference specimen. Locality 3: P94213.
Description. Leaf size: length at least 75 mm, width about 8 mm. Leaf shape: lorate, apex unknown, base acute, petiole unknown. Margin non-entire (toothed), tooth height about 1.5 mm, reclined, sinuses rounded, spacing about 5–10 mm. Venation unclear.

Toothed Margin Type J
(Fig. 16J)

Reference specimen. Locality 3: P94320.
Description. Leaf size: length 62 mm, width 36 mm. Leaf shape: narrow obovate, apex obtuse (bluntly pointed), base cuneate, petiole 23 mm. Margin non-entire (toothed),

tooth height 0.2 mm, spacing about 2 mm. Venation not preserved.

Compound Leaves
(Figs 17–20)

Compound Leaves A, C, D may be Sapindaceae, but no detailed comparisons have been made. Compound Leaf E is trifoliate (Fig. 20A), the leaflets are sessile on the petiole, causing their bases to overlap slightly. The margin is finely toothed. Trifoliate leaves of this general form are common in the Rutaceae, but there are seemingly few with toothed margins as well. *Acradenia franklineae* is an example, but is only toothed on the apical half of the leaflets. A further possibility is with the Cunoniaceae (eg *Pseudoweinmannia lachnocarpa* is grossly similar) but no close comparisons have been made.

Compound Leaf F (Fig. 20B) is represented by a single poorly preserved specimen. The pinnately compound leaf has leaflets which are opposite and the margins appear to be highly sinuous. It is possible this is a fern frond.

Compound Leaf G (Fig. 20C) is represented by a single specimen with a curved, markedly asymmetrical base indicating it is a leaflet from pinnately compound leaf. It shows gross similarity with leaflets in the Simaroubaceae (eg. *Ailanthus integrifolia* B. Hyland) and Meliaceae (eg. *Toona australis* and *Dysoxylum muelleri* B. Gray), but differs in the finely toothed margin. Its identity remains unknown.

Compound Leaf A
(Figs 17-18)

Reference specimen. Locality 2: P94277.
Referred material. Locality 1: P94124, P94110 ?P94199. Locality 2: P94273, P94275, P94276, ?P94258. Locality 3: P94280, P94282–P94285, SB969, SB971, SB974–SB976.
Description. Form imparipinnate. Leaf size: estimated length about 110–120 mm, width about 140 mm. Leaflet size: length 55–100 mm, width 12–30 mm.
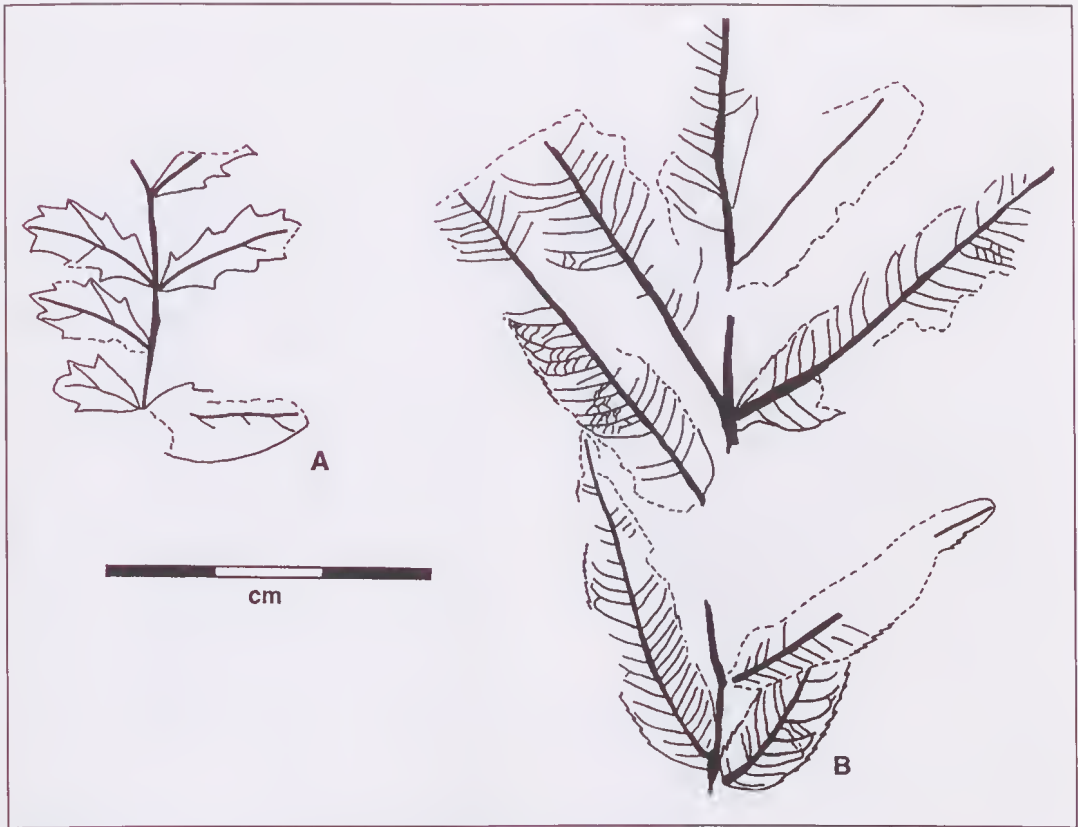
Fig. 19. A, Compound Leaf C, P94281; **B**, Compound Leaf D, P94326.

Compound Leaf B
(Pole and Bowman 1996)

Reference specimen. Locality 3: SB950.

Compound Leaf C
(Fig. 19A)

Reference specimen. Locality 3: P94281.
Description. Form pinnate. Leaf size: preserved length 30 mm, width about 28 mm. Leaflet size: length 9–15 nm, width about 6 mm.

Compound Leaf D
(Fig. 19B)

Reference specimen. Locality 4: P94326.
Referred material. Locality 1: ?P94109. Locality 2: ?P94272.
Description. Form imparipinnate. Leaf size: estimated length 90 mm, width 80 mm.

Leaflet size: length 25-estimated 50 mm, width 7–15 mm.

Compound Leaf E
(Fig. 20A)

Reference specimen. Locality 1: P94100.
Referred material. Locality 1: 94127, P94146. Locality 3: P94279, P94298.
Description. Form trifoliate. Leaf size: length 62 mm, width approximately 65 mm. Leaflet size: length 48–60 mm, width 13–14 mm.

Compound Leaf F
(Fig. 20B)

Reference specimen. Locality 3: P94278.
Description. Form imparipinnate. Leaf size: preserved length about 80 mm, width about 50 mm. Leaflet size, length about 30 mm, width about 20 mm.
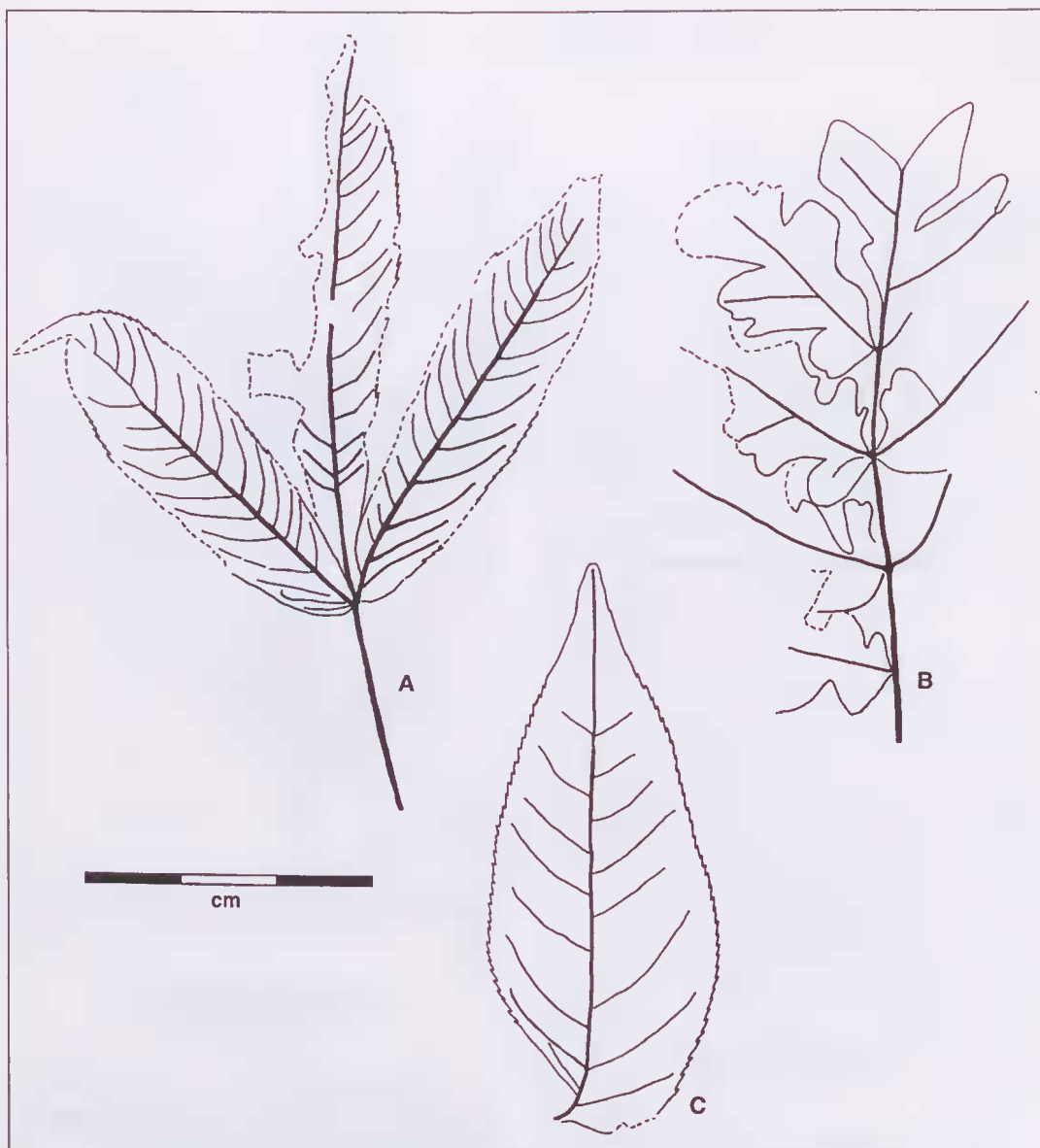
Fig. 20. **A**, Compound Leaf E, P94100; **B**, Compound Leaf F, P94278; **C**, Compound Leaf G, P94126.

Compound Leaf G
(Fig. 20C)

Reference specimen. Locality 1: P94126.
Description. Form presumed pinnate. Leaf size: length and width unknown. Leaflet size: length 62 mm, width 25 mm.

DISCUSSION

Floristics and modern affinities of the assemblages. *Araucaria* section Eutacta is an important component of the assemblages for estimating the present day affinities of the assemblages. Webb (1959) treats *Araucaria* as a 'special life form' to designate two subformations of Australian forests—mixtures of Vine forest or Vine woodland with emergent *Araucaria*. These were termed Araucarian Notophyll Vine forest (ANVF), and Araucarian Microphyll Vine woodland (AMVW) and occur in mesothermal regions with seasonal drought (Webb 1968). While this is the case today,

extinct species of *Araucaria* in the Australian Tertiary occurred under quite different environmental conditions, namely in forests dominated by Podocarpaceae and *Nothofagus* which were clearly much wetter (Bigwood and Hill 1985; Hill and Bigwood 1987; Hill 1990). These elements are clearly absent from the Melville Island assemblages and support the view that present day vegetation types with *Araucaria* in Australia may be reasonable analogues.

The presence of *Brachychiton* and highly dissected *Grevillea* also support comparison with ANVF and AMVW in the sense that they are characteristic of seasonally dry, more open-canopied vegetation. *Brachychiton bidwillii*, a similar leaf form to the Melville Island fossil, is deciduous and occurs in vine thickets and ecotones of vine thicket or vine forest with eucalypt open forest or woodland (Guymer 1988). The possible representation of Sapindaceae and Rutaceae amongst the compound leaved fossils is also consistent. Young and McDonald (1987) note that these two families are among those that often predominate in Araucarian vine forests. Conversely, they noted that Meliaceae and Proteaceae are two which sometimes disappear altogether or become poorly represented. *Ceratopetalum apetalum* does not normally occur in ANVF or AMVW but may occur close by in a different vegetation type. Its possible occurrence (as Toothed Margin Type A) with *Araucaria* in the Melville Island assemblages suggests a wider range of tolerance than shown by the extant species, or that it is another species.

Close comparison with extant vegetation communities probably cannot be made. Some climate types of the Tertiary probably do not exist today, while there is no doubt many plant associations which contained *Araucaria* have become extinct as a result of the intense anthropogenic burning in the drier parts of Australia. Young and McDonald (1987) note the widespread clearing of Araucarian vine forests in recent time. Some of these communities may have been forests which have owed their composition more to very low nutrient status than low rainfall. As a result of more intense burning and extinction of these communities, the only comparable extant vegetation may be in areas of low/seasonal rainfall and relatively high nutrients. A false impression of the climate may be gained. P. Latz (pers. comm.) suggested this might be the case for the Melville Island assemblages.

To test this hypothesis, comparison can be made with other fossil assemblages from areas which were relatively dry and had low nutrient levels. Hill and Merrifield (1993) described an Paleogene macroflora from West Dale in Western Australia which was undoubtedly derived from a very low nutrient substrate. The differences from Melville Island are significant. The authors state a 'clear broad-leaved rainforest component' is present. *Nothofagus* is present, and several specimens of Podocarpaceae were collected and identified to two genera, *Retrophyllum* and *Dacrycarpus*. As noted above, these are absent from Melville Island. At least one species of broad-leaved Lauraceae was present. These are generally as common in typical 'rainforest-type' Tertiary assemblages (pers. obs) as they are in rainforest of Australia today. In the Melville Island assemblages there are no leaves which are considered to be potential Lauraceae. *Gymnostoma* was present in Western Australia, but not in Melville Island. Myrtaceae were prominent in the Western Australia species count (8) but were all of generally elliptical form, compared to the single extremely elongate form of Melville Island *Melaleuca*. Araucariaceae were present, but as *Agathis*, generally confined to wetter environments today than *Araucaria*.

Of the similarities, at the West Dale locality Proteaceae dominated the specimen and species count (11) and Cunoniaceae (*cf. Callicoma*) was present but highly dissected Proteaceae leaves were not found. Hill and Merrifield (1993) suggested that as the climate dried and possibly became hotter, genera such as *Agathis*, the podocarps, and *Gymnostoma* would have become extinct. There is thus no evidence here to support the idea that the Melville Island assemblages are a result of very low nutrient levels under moderate rainfall, but it is suggested that it could have derived from a Paleogene Western Australian-type flora after rainfall decreased.

Another Tertiary fossil flora which would have grown in very low nutrient conditions is

Nelly Creek, from the south edge of Lake Eyre (Christophel *et al.* 1992). This flora again shows similarities with the Western Australian fossil flora. It has *Agathis*, Podocarpaceae, *Gymnostoma*, and numerous entire-margined, elliptical leaves. Proteaceae and Myrtaceae were prominent. It can again be assumed that rainfall was moderately high, with low nutrient levels, and that some form of rainforest developed. To eliminate these taxa and thus to arrive at a Melville-Island type of assemblage, rainfall presumably decreased.

Nearby the Nelly Creek fossils are deposits of 'silcrete floras'. These are fossil leaves in silica-cemented sandstone (silcrete), which are widely distributed across South Australia. Their age is unclear, but in some instances appear to be Eocene. Greenwood *et al.* (1990) reported *Brachychiton*, narrow, sometimes falcate Myrtaceae leaves, as well as toothed leaves possibly similar to the 'Toothed A' leaves described here. Christophel *et al.* (1992) also noted a narrow, linear, entire-margined Proteaceae leaf occurred in the silcrete. I suspect that the silcrete floras may be one of the major keys, not only to the floristic identity of some Melville Island fossils, but also to their age.

Assemblages. The number of individual specimens in the main assemblages is indicated in Table 1. Locality 4 has not been shown as it is essentially just ?fern fronds with a very few angiosperm leaves. Within Locality 1, specimens have been divided as coming from the purple mud facies, or otherwise. The purple mud facies has a distinct assemblage dominated by *Smilax* (this is the only assemblage containing *Smilax*), and 'Toothed A' subdominant. Compound leaves and *cf. Dilobeia /Liriodendrites* are absent from the purple mud facies.

The sediments from Locality 1 which are not purple mud, are heterogeneous, but sandier or siltier, and are more similar to lithologies from Localities 2 and 3. The assemblages from these other lithologies are also similar, with *Smilax* absent, and compound leaves, *cf. Dilobeia /Liriodendrites* and *Grevillea* important. The taxonomic

differences may reflect the different substrates, the purple mud supporting a community requiring higher-nutrient levels than the community occupying sandier substrates.

There is no suggestion that the floristic differences between the lenses were due to anything other than normal spatial heterogeneity or from relatively short-term (i.e. a few hundred years) variations in floristic composition.

Foliar physiognomy. The leaf assemblages have a remarkably distinct physiognomic 'signature'. The assumption is followed here that the physiognomic signature reflects, in some way, the climate in which the original plant communities lived in. Physiognomy of individual leaves is shown numerically in Table 2, and of taxa in Table 3.

The length of leaves was measured, or mostly estimated, in all cases where the leaf was considered complete enough to allow it. Leaflets of compound leaves were treated as individual leaves, but all the deeply divided *Grevillea* leaves were ignored. Their inclusion would probably require measuring the lengths of each lobe, and the statistical value of attempting this on the few leaves is dubious. The over-all average leaf length of 64 mm indicates that the leaf area falls within the microphyll category (Webb (1959) gave the boundary between microphyll and notophyll leaves as 76 mm for leaves of lanceolate or elliptical shape). This is relatively small - Webb (1959) documented that Australian tropical and subtropical forests, where conditions were optimal, had significant proportions of notophyll, and even mesophyll leaves, whereas microphyll leaves became more important as temperatures cooled, or rainfall became limiting. Likewise, Specht and Womersley (1979) noted that in Borneo, under presumably optimal rainfall and temperature, Dipterocarp forests had an average leaf size of mesophyll, whereas the 'kerangas', on nutrient poor soils, had an average leaf size of notophyll. The small leaf size of the Melville Island leaves could be a reflection of low nutrient levels of their substrate. The leaves of the purple mud

Table 1. Specimen counts for each assemblage. Locality 4 is omitted as it contains mainly the ?fern type and one Compound Type D leaf.

	Total	Locality 1 purple mud facies	Locality 1 not purple mud	Locality 2	Locality 3
Araucariaceae	12	9			3
Cupressaceae	4	1	3	1	3
Brachychiton	2	1	1		
cf. Dilobeia	20		4	1	12
Grevillea cf. whitiana	30	5	11	4	10
G. cf. longifolia					1
G. cf. dryophylla					1
?Legume	1	1			
Melaleuca	12	9	4		1
Smilax	38	38			
Entire A	20	4	3	2	9
Entire B	2	3	1	1	
Entire C	1		1		
Entire D	1		1		
Entire E	1	1			
Entire F	5	3	2		
Toothed A	44	24	14	3	2
Toothed B	3		1	1	1
Toothed C	1	2			
Toothed D	2	1			1
Toothed E	4		1		1
Toothed F	1				1
Toothed J	1				1
Toothed G	1				
Toothed H	1				
Toothed I	1				1
Compound A	14		1	4	9
Compound B	1				1
Compound C	2		1		1
Compound D	3		2		
Compound E	4		1		2
Compound F	1				1
Compound G	1		1		
Unallocated	18	4	4	7	4

facies, which might be expeeted to have a higher nutrient level than the sandier substrates, are larger. They have an average length of 75 mm which however, is still within the microphyll category. Leaf length of the fossils suggests temperature and/or rainfall was suboptimal.

It has long been observed that tropical rainforest is overwhelmingly dominated by leaves whieh have entire margins. Richards (1952) provided outline drawings of tropieal rainforest leaves to emphasise this, as well as their overall similarity of shape - mostly oblong-laneeolate to elliptical. When it comes to estimating the proportion of entire margined leaves in the Melville Island assemblages, a difficulty arises, whieh, in itself, suggests something was unusual about the environment. In short, the typieal tropical rainforest shape of leaf is rare. Whereas *cf.*

Table 2. Physiognomic summary based on individual leaves and leaflets.

	Overall total	Locality 1	Locality 2	Locality 3	Locality 1 purple mud	Locality 1 not purple mud	Overall total except purple mud
Angiosperm leaves	297	163	35	90	96	68	201
Average length	64mm	71mm	87mm	52mm	75mm	60mm	59mm
Entire (no lobes)	27%	41%	9%	11%	56%	16%	14%
Entire (no lobe/linear)	15%	27%	3%	Nil	43%	9%	2%
Toothed	49%	42%	66%	52%	28%	59%	58%
Lobed	18%	13%	14%	24%	6%	24%	23%
Compound leaflets	27%	14%	46%	39%	Nil	34%	40%

Table 3. Physiognomic summary based on taxa.

Angiosperm taxa with leaves	30%
Entire (no lobes)	27%
Entire (no lobes, not linear)	17%
Toothed	57%
Lobed	10%
Compound	23%

Dilobeia/Liriodendrites has an entire margin, it is deeply bi-lobed, the *Grevillea*s do not have teeth, but are deeply lobed/disseeted. The 'Entire Margin A' and the *Melaleuca* leaves are entire, but are extremely elongate. Excluding the lobed, or lobed and elongate leaves, entire margined proportions are extraordinarily low: overall between 11% and 19% of the taxa, or 15% and 30% of individuals.

The purple mud of Locality 1, dominated by the entire-margined *Smilax*, still has only between 40% and 60% of individuals with entire margins. However, the real amounts of *Smilax* and 'Toothed Leaf B' in the purple mud, and their proportions to the rarer taxa, will be higher than the number actually catalogued, beeause of many over-lapping and fragmentary speeimens, and the need to choose which individuals to expose completely. If the amounts of these two taxa were up to ten times more than those eatalogued, a probable over-estimate, the entire-margined proportion would rise to a little over 60%.

Excluding *Smilax*, entire margined leaves which are unlobed or not elongate, are virtually absent. Normally (e.g. Bailey and Sinnott 1916; Wolfe 1979) entire margined leaves are contrasted with toothed leaves, and low figures for entire margins are taken as indieating eool conditions. This eannot be done directly for these assemblages because of the lobed leaves which are not ineluded in either category. Toothed margin perecntages were ealculated separately based on the 'Toothed' taxa and the 'Compound' leaves, all of which are toothed. Over all, toothed leaves are about double, or more, than entire margins, on taxon or individual eounts. Only in the purple mud facies do these figures reverse. The over-all figures suggest relative eoolness. The figures from the purple mud might be explained by the overwhelming dominanee of *Smilax*, a elimber and not a eanopy tree, unduly skewing what would be a dominance by toothed types. The number of leaflets from eompound leaves in the assemblages, is striking. Overall the figure is 27%, but they are notably absent from the purple mud. Omitting this assemblage, they form 58% of all individuals, and 23% of all taxa. Even this is probably an underestimate, as it is based on taxa which are clearly eompound - other forms, like Toothed D and Toothed 1 may also be leaflets.

Such a high proportion of eompound leaflets is unusual in a fossil assemblage - in most eases it might be expected that the leaves disaggregated into their leaflets during taphonomic processes. The figure may also be giving some form of physiognomie signal on the environment. For instance, Bews (1925, 1927) found in

southern Africa that the percentage of tree species with compound leaves was greater in areas with seasonal drought than well-watered regions. Webb (1959) found the highest percentage of individuals with compound leaves in Australian forests (c. 60%) was in Araucarian Microphyll Vine woodland. This is significant given the presence of *Araucaria* throughout the assemblages. Givnish (1978) reasoned that compound leaves were 'adaptive in at least two sorts of environmental contexts: in warm seasonally arid situations that favour the deciduous habit, and in light gap and early successional vegetation where rapid upward growth and competition for light favour the cheap throwaway branch'. The later context is unlikely to be the controlling factor here. The purple mud assemblage, dominated by *Smilax*, is the most likely to be sampling such an environment, but compound leaves are absent from it.

Pronounced lobing is present on three taxa: *cf. Dilobeia/Liriodendrites*, *Brachychiton*, and Grevillea. Overall, and in most assemblages it is close to 20% (10% of all taxa), except in the purple mud, where it is 6% and probably reflects the absence of cf. *Dilobeia/Liriodendrites*. Wolfe (1993) concluded that lobing is most characteristic of microthermal environments and was common in open-canopy vegetation. In Australia, as noted above, these forms of *Brachychiton* and *Grevillea*, and *Bauhinea*, as a possible physiognomic analogue of *cf. Dilobeia/Liriodendrites*, are characteristic of warm and seasonally dry vegetation.

It is important to understand that evidence of rainfall seasonality in Australia's far north during the Paleogene (see below for age) does not contradict the hypothesis of the tracking latitude of Sub Tropical High Pressure (STHP) cells overtaking Australia from the south in the Miocene (Bowler 1982; Pole 1993). The limits of the migrating STHP hypothesis are likely to be in the Oligocene when Australia's continued northward movement caused the formation of the circumpolar ocean current (Kennett 1977). Before this, boundary conditions were completely different—the zonal atmospheric system as we know it may not have existed.

In summary, the physiognomy confirms the conclusions of Pole and Bowman (1996), that the climate was 'warm, but not tropical, and rainfall was probably seasonal'.

Reassessment of the age. The Van Diemen Sandstone is still not precisely dated. No carbonaceous lithologies were encountered on this expedition, so palynology is unlikely to be of direct use, though has not been ruled out. No marine fossils were found either. However, two lines of reasoning suggest the formation may be of Paleogene age, rather than Neogene.

Firstly, the sediments appear to have been deposited by a constantly flowing stream, rather than one of intermittent or ephemeral nature. From a variety of palynological evidence, Australia was progressively drying out during the later Tertiary, and streams were likely to have become more seasonal. Megirian (1992) interpreted the Miocene Carl Creek Limestone of Riversleigh, northwestern Queensland, as accumulating under relatively dry, perhaps semi-arid conditions. This is consistent with the palynological evidence. Other Miocene limestones across northern Australia indicate these conditions were widespread at the time and do not suggest a stable catchment supply for large, stable rivers.

Secondly, the climate suggested by the leaf physiognomy - warm, but not tropical - would be more consistent with an older age, when Australia was situated at more southern latitudes. Feary *et al.* (1991) inferred subtropical conditions for northernmost northeast Australia throughout the Paleogene based on carbonate sedimentation, with tropical conditions not being realised until the Early Miocene. Earlier inferences of tropical conditions for this region in the Paleogene by Davies *et al.* (1989) are apparently incorrect. In addition, Thunell *et al.* (1994) have provided evidence that even during the height of the last glaciation, temperatures in the tropical Western Pacific remained much as they are today. This suggests that land temperatures at tropical latitudes in Australia have also remained much the same throughout the Tertiary, and that the greatest fluctuations have been polewards.

In addition, work in progress on the Paleogene fossil flora of Redbank Plains,

near Brisbane, has shown deeply disseeted Proteaeeae leaves like *Grevillea* sp. *cf. G. whitiana* are a feature. Perhaps these kind of Protcaceae were a dominant feature of Paleogene vegetation in northern Australia. They do not appear to have been eommon in southern fossil floras.

Future work. It is elear from the brief exploration that more fossil localities exist on Melville Island, and may be widespread. Future collecting would extend the taxonomic database, and there is mueh scope for a detailed sedimentologieal analysis.

A much better understanding of the climate will result from sampling present day plant communities with transeets from those growing on poor substrates to those on more nutrient rich ones. The lowlands of Borneo will make an excellent study area for this approaeh.

A more preeise date for the fossils is now of utmost priority. One approach would be to try and trace the Van Diemen Sandstone offshore in drill cores, where microfossils may still be preserved. Finding floristic matches with specimens in other, better dated fossil assemblages in northern Australia, is another.

SUMMARY

The fossil flora of Melville Island is an extremely important addition to the paleobotanical and paleoclimatie knowledge of Australia. It is so far the best known Tertiary site with plant macrofossils from the northern 50% of Australia and thus provides an important control point for developing biogeographie theories. Although deep weathering has destroyed much valuable detail, enough remains to be useful. The genera which have been identified ean be related to the present vegetation of Australia, and point towards drier, more seasonal forests. The foliar physiognomy is distinet and tells a similar story. The age of the deposit is still uneertain, but the evidence is pointing towards the Paleogene, perhaps Paleocene or Eocene. The evidenee of seasonal elimate so early in the Tertiary of Australia is the most important eonclusion of this work.

ACKNOWLEDGMENTS

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